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INHERITANCE IN CROSSES OF JERSEY AND HOLSTEIN-FRIESIAN WITH ABERDEEN-ANGUS CATTLE. I. HORNS AND SHAPE OF SKULL[1]

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A CATTLE cross breeding experiment to study the inheritance of dairy and beef qualities was carried out between 1912 and 1933 by the Wisconsin Agricultural Experiment Station under the supervision of the senior author. Animals of the polled self-colored Aberdeen-Angus breed were crossed to horned Jerseys and Holstein-Friesians, an F_2 generation was raised and backcrosses and some other crosses were made. In addition to data on yield and composition of the milk, and on weight and body measurements of the animals, external characters, such as the horned or polled condition, color and white markings, were also recorded. In this paper data on horns and shape of skull will be presented and compared with similar data from other experiments, and the results will be discussed in relation to physiology of development as well as from a genetic point of view. The genetics and color of white markings will be discussed in Part II, and some quantitative characters in Part III.

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Foundation Animals

The experiment started with one male and two females of each of the Jersey and Aberdeen-Angus breeds. Later other Jersey bulls from the station herd were used for backcrossing purposes. In 1920 it was decided to substitute the Holstein-Friesians for Jerseys in order to obtain greater difference between the two parental breeds in body size as well as in milk yield and butterfat percentage. Funds were not available for buying high quality purebred animals when foundation stock for the

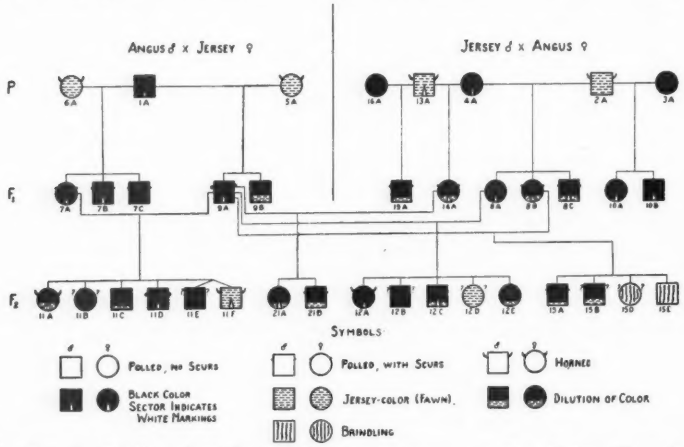

Fig. 1. Mating chart for the Jersey × Angus cross: Foundation, F_1 and F_2 animals, with the horn and color characters indicated.

Holstein × Angus cross was procured, and therefore advantage was taken of the fact that recessive red offspring occasionally appear in both breeds (Cole and Jones, 1920). Four of the six foundation Angus cows bought for this cross were self red, and all the Holstein cows were red and white. Every animal was, however, from registered parents of the standard color and type and must therefore be considered as equivalent to purebred. No bulls were bought for this cross, the Angus and Holstein bulls from the station herd being used

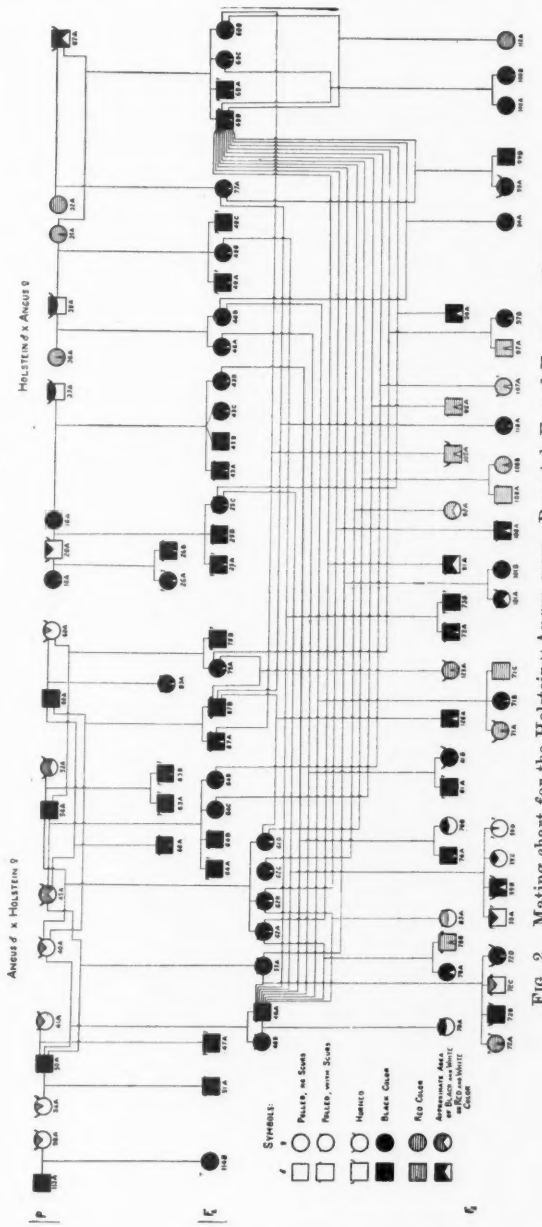

FIG. 2. Mating chart for the Holstein × Angus cross; Parental, F_1 and F_2 generations.

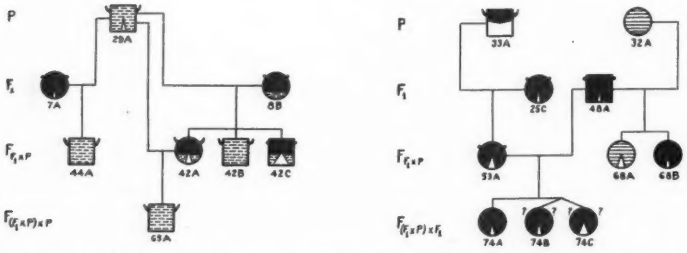

FIG. 3. Mating chart for backcrosses. Left: Jersey × Angus cross. Right: Holstein × Angus cross.

throughout the experiment. All these bulls were registered and conformed to the standards of their respective breeds. In Figs. 1–5 mating charts are presented for the experimental herd showing the different crosses made and the phenotypical expression of the characters studied. On the charts we have recorded only the foundation cows which gave birth to offspring.

RECORDING OF DATA

The animals in the experimental herd were numbered consecutively as they were added to the herd by purchase or breeding. When two or more animals were obtained from the same parents they all received the same number, but the individual full brothers and sisters were distinguished by letters, *e.g.*, 7A, 7B, 7C, etc. All breeding data were recorded chronologically, and in addition a breeding record was kept for each individual cow or

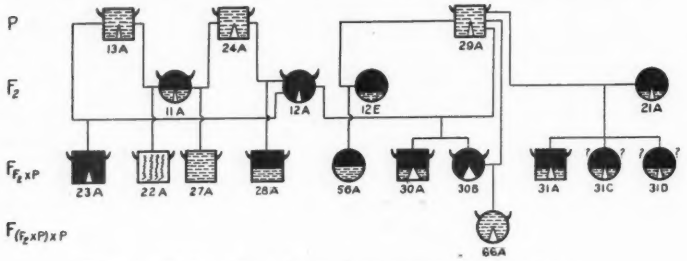

FIG. 4. Mating chart for various crosses, Jersey × Angus.

bull. Photographs were taken and descriptions made of the animals at certain intervals. Descriptions of the horn character of the living animals were made and when the animals were photographed, attempts were made to show as well as possible the size and shape of horns and the development of scurs. In order to facilitate a study of the causal foundation of scurs, the skulls have, as a rule, been preserved after slaughter of the animals. Due to various circumstances this material is, however, not quite complete.

In the mating charts the color is noted for all cross-bred calves carried to full term, but whether an animal

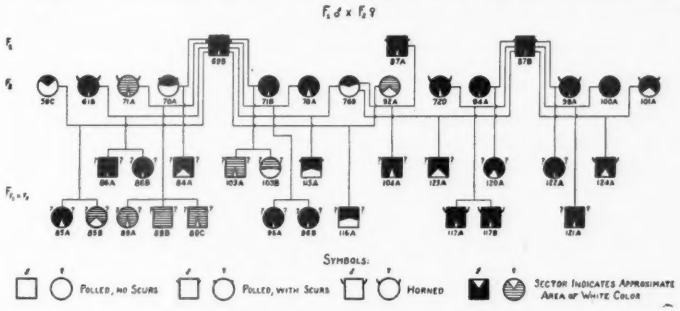

FIG. 5. Mating chart for various crosses, Holstein × Angus.

was to be polled, horned or scurred is not known for calves which were vealed at an early age. According to Terho (1918) it should be possible to diagnose the horned character in a calf immediately after birth. While this may be true, the development of scurs can not be determined at such an early stage. At the age of three months the horned condition can be diagnosed with absolute certainty, although the degree of development of scurs in polled animals may still be doubtful. At one year of age the scurred condition is clearly established. All cases where the horned condition was not definitely known are denoted on the mating charts (Figs. 1–5) by question marks; animals so denoted are not included in

the data, which show the segregation of the horned character. The animals which were thus excluded would probably have been distributed at random in the different classes, polled, scurred and horned, because they were eliminated at a stage when no diagnosis of the horned condition could be made. The total number of excluded calves is 43; of those 21 were aborted, or stillborn, or died shortly after birth, and 22 were vealed at an early age.

The F_1 and F_2 Generations, Backcrosses and Other Crosses

The foundation animals of the Aberdeen-Angus breed,

TABLE 1

Occurrence of Polled, Scurred and Horned Animals in the F_1 and F_2 Generations, Backcrosses and Other Crosses

Crosses	Males (bulls and steers)			Females			Total
	Clean polled	Scurred	Horned	Clean polled	Scurred	Horned	
F_1:							
Jersey ♂ × Angus ♀	1	2	–	2	2	–	7
Holstein ♂ × Angus ♀	1	4	–	7	2	–	14
Total: Horned ♂ × polled ♀	2	6	–	9	4	–	21
Angus ♂ × Jersey ♀	1	3	–	—	1	–	5
Angus ♂ × Holstein ♀	–	6	–	6	5	–	17
Total: polled ♂ × horned ♀	1	9	–	6	6	–	22
Total F_1	3	15	–	15	10	–	43
F_2:							
Jersey × Angus	3	3	1	2	—	2	11
Holstein × Angus	6	7	3	13	2	6	37
Total	9	10	4	15	2	8	48
Backcrosses:							
Jersey ♂ × F_1 ♀♀ (Sc)	–	1	2	—	—	1	4
Holstein ♂ × F_1 ♀♀ (Sc)	–	—	–	—	1	–	1
Total	–	1	2	—	1	1	5
F_1 ♂ (Sc) × Angus ♀	–	—	–	2	—	–	2
Other crosses:							
Jersey ♂ × Extracted H ♀♀	–	—	5	—	—	2	8
Jersey ♂ × Extracted P ♀♀	–	—	1	1	—	–	2
F_1 ♂ (Sc) × Backcross Sc ♀	–	—	–	1	—	–	1

H, horned, P, polled, and Sc, scurred condition.

bulls and cows, were all clean polled, and those of the Jersey and Holstein-Friesian breeds all had normally developed horns. The crossbreeding results in the F_1 and F_2 and backcross generations are shown in Table 1. None of the F_1 animals developed horns, but about 60 per cent. were scurred. Scurs are more frequent in the males than in the females, particularly in the Holstein $\times$ Angus cross. In F_2 there were 24 animals described as "clean polled" and 12 as scurred, the total number of polled thus being 36. The number of horned F_2 animals was 12 and the fit to the 3:1 ratio is, therefore, perfect.

In Table 2 we have compiled data on the segregation in

TABLE 2

THE F_2 SEGREGATION IN CROSSES BETWEEN HORNED AND POLLED BREEDS OF CATTLE

Investigators breeds	Polled (clean polled and scurred)	Horned	Total
Lloyd-Jones and Evvard (1916) Shorthorn × Galloway	16	5	21
Watson (1921) West Highland × Angus	18	7	25
White and Ibsen (1936) Holstein × Galloway	20	9	29
Total	54	21	75
Wisconsin experiment Holstein or Jersey × Angus	36	12	48
All data combined	90	33	123

F_2 of the horned and polled condition in other cross-breeding experiments. The total obtained in 54 polled and 21 horned animals, whereas the expected numbers would be 56 polled and 19 horned. The deviation from the 3:1 ratio is small and insignificant. Combining the data from Tables 1 and 2 we get 90 polled and 33 horned (expected 92:31), a very close fit to the theoretical 3:1 ratio.

Fig. 6 shows three preserved skulls from foundation animals in the crossbreeding experiment, and Figs. 7 to 10 show scur development and skulls for a number of F_1 individuals. The scurs in the bulls range from very large to small and inconspicuous (Fig. 7), but the bony excres-

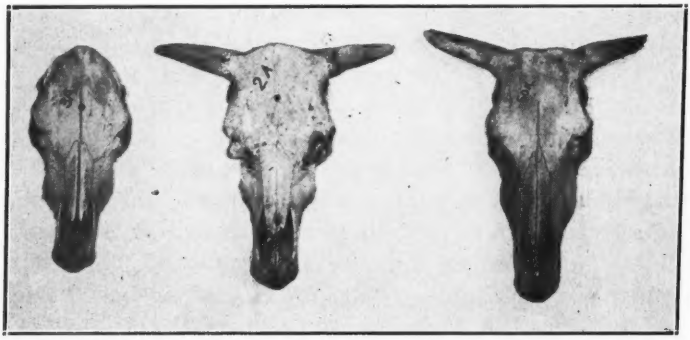

FIG. 6. Skulls of three foundation animals in the cross-breeding experiment: Angus ♀ 3A, Jersey ♂ 2A and Holstein ♀ 60A.

cences at the horn loci are very large in all the bulls. Fig. 9 shows two F_1 cows from the Jersey × Angus cross, one with and one without scurs; the cow without scurs (8A) had, however, bone protuberances at the horn locus. In Fig. 10 two clean polled F_1 skulls from the cows 64D and 69D of the Holstein × Angus cross are shown, and two F_1 skulls (cows 48B and 62C) with bone protuberances. Fig. 11 shows three extracted horned F_2 animals, and Fig. 12 shows preserved skulls from F_2 cows. The size and shape of the horns of F_2 animals may be quite different from that in the horned parental breed. The horned F_2 segregates from the Angus x Jersey cross had much larger horns than the Jerseys. In the Holstein x Angus cross the change in size and shape of horns in the F_2 generation, compared to purebred Holsteins, was less pronounced, but it could be noted here also, *e.g.*, in the cow 72D (Fig.12) who had rather wide and coarse horns. Apparently the horn growth was considerably influenced by genetic factors brought in by the polled Angus breed. The steers had longer and more slender horns than the bulls. Polled steers showed a corresponding difference in scur development, compared with non-castrate polled males.

When scurred F_1 cows in the Wisconsin herd were backcrossed to horned bulls (29A and 33A, Fig. 3) 3 horned and 2 polled calves were obtained, and a backcross of the scurred F_1 bull 48A to the clean polled Angus cow 32A gave two clean polled female calves. In cases where horned F_2 cows were backcrossed to horned Jersey bulls, all the offspring, 8 in number, were horned. Two clean polled F_2 cows, backcrossed to a Jersey bull, produced, however, one horned and one polled offspring. Assuming that these extracted clean polled cows were heterozygous for polledness, the results are in perfect agreement with the hypothesis that the polled and horned characters depend on one allelic pair of genes, the gene for polledness being rather strongly, but not completely dominant to that for the horned condition, as sugegsted by Bateson and Saunders (1902) and accepted by most later writers on the horn inheritance in cattle.

The Development of Scurs in Crossbred Animals

The figures in Table 1 show that more than half of the F_1 animals in both crosses had scurs, and also that scurs were more common among the males than among the females. It should be pointed out, however, that "scurred" in this table means that the animal had visible keratinous developments, *i.e.*, there was at least a definite beginning of horn sheath formation. All other polled animals are classified as clean polled, although some few may have had very small scurs which escaped detection at the description of the living animal. Several of the animals which were classified as clean polled showed small protuberances on the frontal bones at the horn loci. These protuberances may be distinguishable on the living animal (*e.g.*, the F_1 cow 8A, Fig. 9) but can be more clearly seen on the preserved skulls. There are, however, cases in which F_1 skulls appeared just as clean polled as those of the purebred Angus animals. As ex-

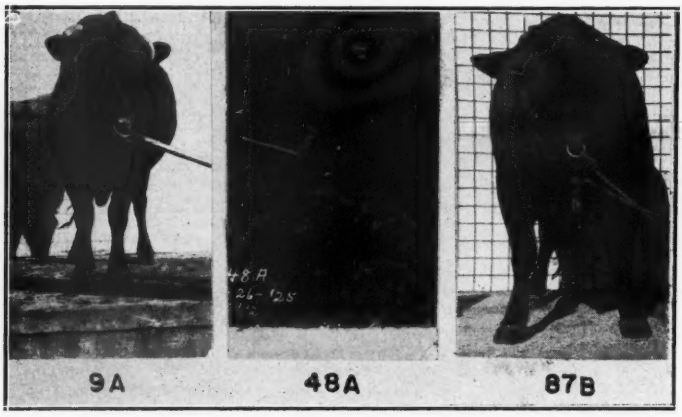

FIG. 7. Three different types of scurs in F_1 bulls: 9A (Jersey × Angus) with very large scurs, 48A with rather small scurs and 87B with moderate sized scurs (48A and 87B: Holstein × Angus).

amples of such skulls we have the F_1 Jersey × Angus cow 10A and the Holstein × Angus cow 64D and 69D (Fig. 10). It is questionable whether any skulls of the F_1 steers can be considered as clean polled. In females, at any rate, a clean polled skull, without scurs or bone protuberances, can not be taken as decisive evidence of homozygosity for polledness, although it is probable that in a mixed population the large majority of clean polled cows would prove to be homozygous for the polled character, and conversely, the cows with scurs would be heterozygous (*cf.* Terho, 1918).

There is some confusion in the literature as to the real difference between horns and scurs. Gowen (1918) speaks of "loose scurs" and "tight scurs," "loose" horns and "solidly attached" horns but leaves the reader to guess the difference between "tight scurs" and "loose horns. Wilson (1909) writes regarding loose scurs that "there is no developed core or bony outgrowth beneath the scurs"; and Lloyd-Jones and Evvard (1916) make a similar statement. These statements are, however, not

in agreement with the facts. In the Wisconsin cross-breeding experiment all skulls of cross-bred animals were carefully examined. Dove (1935) who was in charge of the experiment as an assistant for several years, boiled the scurs until the keratin sheath was dissolved, and he found bony cores in all scurs over 2 cm in length. The largest scurs approached the shape of normal horns and contained *ossa cornua* as large and as regular in formation as any attached horn spike in a similar sized sheath, whereas the smallest scurs appeared as flat corneous scales, ranging in size down to 0.5 cm in diameter. In living females the scurs were sometimes found only after a careful search as they could not always be detected by touch. Dove also found that all scurred animals had bony excrescences at the horn loci. The development of these excrescences does not seem to be correlated with the size of the scurs carried.

All F_1 bulls which were raised to sexual maturity had scurs, and in one case, the Jersey $\times$ Angus F_1 bull 9A (Fig. 7), the scurs were very large, 6 and 7 inches long, respectively. These scurs were loose, however, and not attached to the frontal bones (*cf.* Fig. 8). Another F_1

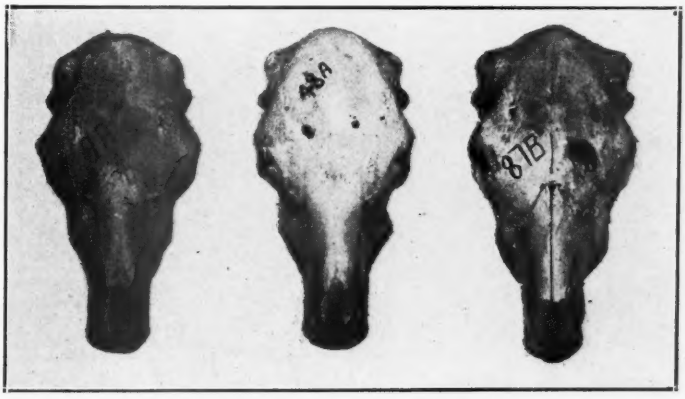

FIG. 8. Preserved skulls from the same F_1 bulls as shown in Fig. 7.

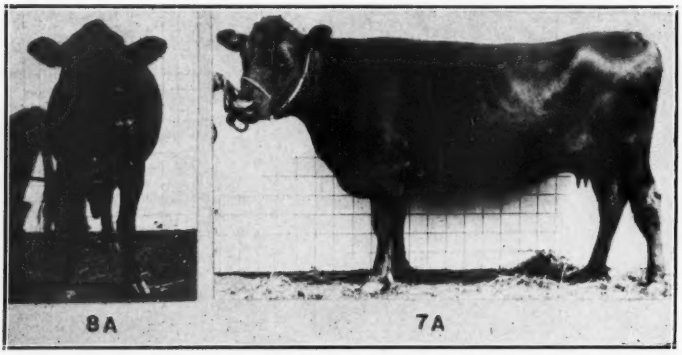

FIG. 9. Two F_1 cows from the Jersey × Angus cross. Cow 8A has no scurs but marked bone protuberances on ossa frontale, whereas 7A has small loose scurs.

bull from the same cross, 7B, had, however, very small scurs, which were hardly visible externally. Among the F_1 bulls from the Holstein × Angus cross 48A, 51A and 69B had only small visible scurs but rather heavy bone protuberances. The fourth bull from this cross, 87B, had larger scurs, about three inches long, and very pronounced bone protuberances (Figs. 7 and 8).

None of the F_1 steers had as large scurs as had the bulls

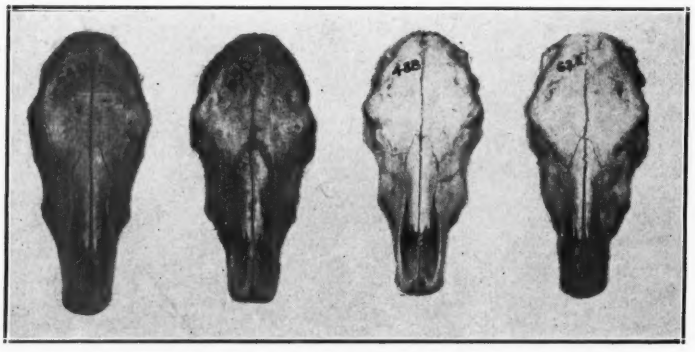

FIG. 10. Two clean polled F_1 skulls (64D and 69D) and two skulls from scurred cows (48B and 62C) with bone protuberances; all skulls are from the Holstein × Angus cross.

9A and 87B but this may be due partly to the fact that the steers were slaughtered before reaching maturity whereas the bulls were not; the oldest steer was 1 year and 10 months old at the time of slaughter. The bulls had also larger and coarser bone protuberances on the skull than the steers. That there is a difference between the male and female sex in the degree of development of horns and scurs is observed by several authors and seems to be a general phenomenon (Landauer, 1925; Churchill, 1927; Black, 1936).

In the F_2 generation all males were castrated at an early age. Two Holstein $\times$ Angus steers, 72C and 78B,

FIG. 11. Extracted horned F_2 animals. The two animals to the left (Steer 71F and cow 11A) are from the Jersey $\times$ Angus cross, and the cow to the right is from the Holstein $\times$ Angus cross.

had fairly large scurs, 2 to 3 inches in length, and the F_2 Jersey $\times$ Angus steer 11D also had rather large scurs. The skull of the steer 78B showed pronounced bone protuberances. None of the F_2 cows had large scurs. Several F_2 cows and steers had a clean polled skull, but it is not known whether the F_2 cows with clean polled skull, *i.e.*, without bone protuberances, were homozygous polled.

SHAPE OF THE SKULL

Some characters of the skull seem to be correlated with the polled and horned condition and therefore we present in Table 3 measurements of the skulls of foundation

and F_1 and F_2 animals. Fig. 13 shows how these measurements are taken on the preserved skull, except for the width at *fossa temporale,* which measurement is taken on the occipital surface of the skull. We have also calculated ratios between some of these measurements, as such ratios give a better indication of the shape of the skull than does any single measurement. No steers, and no cows below three years of age at time of slaughter, are included in the table. No skulls of the foundation Jersey cows or of Holstein bulls were saved.

The figures presented in Table 3 show that the Jersey and Angus bulls had skulls of fairly similar shape, except

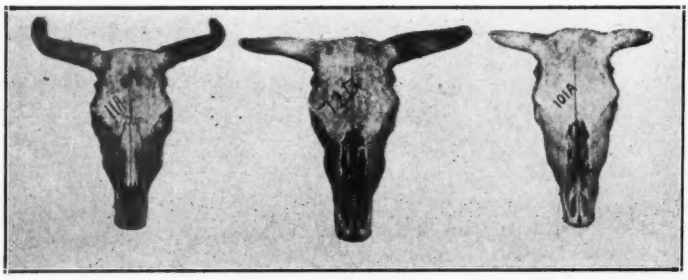

FIG. 12. Skulls of extracted horned F_2 cows: 11A is from the Jersey × Angus, and 72D and 101A from the Holstein Angus cross.

for the presence of horns in the former; both belong to the brachycerous type. The average measurements and ratios for five F_1 Jersey × Angus cows come very close to the corresponding averages for the six foundation Angus cows. None of the differences is statistically significant.

Between the averages for the foundation Holstein and Angus cows on the other hand there are significant differences in the length of the skull and in the posterior width at the *fossa temporale.* The ratios involving these two measurements also differ significantly. The skull of the Holstein cows is longer and proportionately narrower than that of the Angus cows. In the F_1 generation there

is a distinct and significant tendency to dominance of the long-headed primigenius type of skull of the Holstein over the short, brachycerous skull of the Angus. The length-orbital width index of the Angus and F_1 cows is also significantly different, but between the skulls of the Holstein and F_1 cows there are no significant differences. When we compare the F_1 cows of the Holstein $\times$ Angus with those of the Jersey $\times$ Angus cross we also find, on the average, significantly longer skulls and smaller

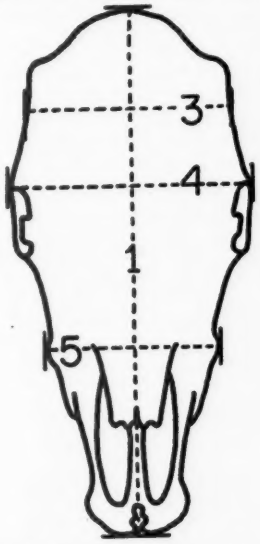

FIG. 13. Diagram showing how the measurements of the skulls are taken: 1 length of skull, 3 frontal width, 4 orbital width, 5 maxillary width.

length-orbital width index in the former group. This fact supports the conclusion that the primigenius type of the Holstein skull is a dominant character.

In Table 3 the F_2 cows from both crosses are grouped according to presence or absence of horns. The skulls of the two horned F_2 Jersey $\times$ Angus cows are longer than the skulls of the polled cows from the same cross, and in the horned F_2 Holstein $\times$ Angus cows the skulls

are, on an average, a little longer than those of the polled cows, but the difference is not statistically significant. It is, therefore, uncertain if any correlation exists between the length of the skull and the polled or horned characters. In all horned cows, however, the posterior width of the skull at the *fossa temporale* is larger than in the polled cows. This measurement seems therefore to be correlated with the presence of horns. The polled skull

TABLE 3

MEASUREMENTS OF SKULLS OF FOUNDATION AND CROSSBRED ANIMALS, CENTIMETERS

Animals	H = horned P = polled	No. of animals	Length cm.	Width cm.				Ratios expressed in per cent		
				Temporal	Frontal	Orbital	Maxillary			
			a	b	c	d	e	c:a	d:a	b:d
					Means					
Bulls:										
Jersey 2A	H	1	50.0	17.0	18.9	25.4	17.1	37.8	49.0	69.4
Angus 1A	P	1	50.2	16.2	20.2	26.1	17.3	40.2	52.0	62.1
F_1 J × A av.	P	2	49.4	16.3	19.5	25.5	17.2	39.5	51.6	63.7
F_1 A × A av.	P	2	54.0	19.0	20.2	26.3	19.3	38.6	48.8	72.0
Cows:										
F_1 J × A av.	P	5	46.2	11.5	16.2	21.4	15.7	35.5	46.5	53.6
F_2 J × A av.	H + P	4	45.1	12.1	16.4	21.4	15.5	36.4	47.5	56.2
Angus av.	P	6	46.0	11.6	15.7	21.1	15.3	34.1	46.0	55.1
Holstein av.	H	6	50.1	13.4	15.9	21.3	15.6	31.8	42.5	63.0
F_1 H × A av.	P	12	49.3	12.5	16.3	21.6	15.9	33.2	43.8	58.1
F_2 H × A av.	P	10	48.3	12.0	16.2	21.3	16.0	33.6	44.2	56.3
F_2 H × A av.	H	3	50.9	14.7	16.9	22.1	16.5	33.1	43.3	66.6
					Standard deviation					
Angus ♀♀	P	6	0.95	0.71	0.42	1.05	0.40	0.77	1.62	1.03
Holstein ♀♀	H	6	2.06	1.24	1.13	0.88	0.77	1.87	1.17	4.41
F_1 H × A ♀♀	P	12	0.81	0.72	1.17	0.36	1.02	0.97	0.64	3.20
F_2 H × A ♀♀	P	10	1.62	0.65	0.86	0.51	1.01	2.13	1.80	3.66
F_2 H × A ♀♀	H	3	2.45	0.72	1.10	1.20	1.18	1.55	0.90	1.14
Total F_2	H + P	13	1.97	1.39	1.29	0.33	1.05	1.65	1.14	7.29

diminishes in width towards the poll while the horned skull increases in width at the horn base. The standard deviation in skull length is greater in the F_2 than in the F_1 generations (diff. 1.16 ± 0.36), but if long skulls are associated with presence of horns a greater variation would be expected even without segregation in the polled class. Curson (1937) points out that debudding young calves causes a pronounced change in the shape of skull

of the mature animal. The standard deviation in skull length of the 12 F_1 Holstein $\times$ Angus cows is 0.81 ± 0.17 cm and for 10 polled F_2 cows of the same cross 1.62 ± 0.36 cm. The difference in standard deviation is 0.81 ± 0.40 cm, which means that it is on the borderline to statistical significance. It may be taken to indicate that segregation of head length has occurred in the polled F_2 cows. It should be pointed out, however, that the foundation Holstein cows were rather heterogeneous in regard to this character; the standard deviation for the group of 6 cows being 2.06 ± 0.60 cm.

Discussion

The hypothesis of monohybrid inheritance of polledness, scurs and horns has been questioned by some investigators, especially by White and Ibsen (1936). Smith (1927) concluded that the dominance of the polled character is sex-limited or that it is due to modifying genes, which would account not only for the higher frequency and greater development of scurs in the male than in the female but also for reported cases of horned F_1 individuals from crosses between horned and polled breeds (Lloyd-Jones and Evvard, 1916; Gowen, 1918; Watson, 1921; and Smith, 1927). In one of these papers (Lloyd-Jones and Evvard) several of the polled cows reported were not purebreds but grades, and they may have been heterozygous for the polled character. Watson reported one F_1 bull which developed "short stout horns which grew at an abnormally slow rate." It is not stated whether the horns were loose or fixed to the skull, but Watson writes 'There could be no doubt that this animal, like the other F_1 crosses, was heterozygous for the polled character." In regard to purebred Angus cattle he states that horns or scurs "were once comparatively common but have now been all but eliminated by selection." Watson also makes the statement that "it appears certain that the degree of dominance of the polled

character in the male varies according to the particular breeds employed." Gowen reported one case where a purebred Aberdeen-Angus bull, mated to horned cows, produced seven polled females and one polled male, six males with loose and three with tight scurs, and one male with heavy horns. This result of 17 polled: 1 horned may seem difficult to reconcile with the monohybrid 1: 1 ratio, assuming that the Angus sire was heterozygous for polledness but would not appear to necessitate a new hypothesis to explain horn inheritance. Smith reported some observations in two herds in Northern Rhodesia where crosses were made between purebred Aberdeen-Angus bulls and native cows. The F_1 heifers were all polled but most of the F_1 bulls had "distinct horns or buds." No further description of the horns and scurs is given, and numbers are presented only for one of the herds. According to Smith the native Africander cattle used in this cross, probably of the Bos zebu type, were not all "purebred" but some of them carried blood from the ordinary domestic breeds, if horned or polled is not stated.

White and Ibsen (1936) reviewed these cases and reported a cross between purebred Galloways and Holsteins. In this cross 15 F_1 animals were obtained, eight polled females and seven males; four of the males had scurs and three were polled. The F_2 ratio, as seen in Table 2, was 20 polled: 9 horned. White and Ibsen find it evident that "the polled character is due to a single dominant gene." They continue, however, "It is not so evident what constitutes the recessive allelomorph of this gene, nor is there as yet a satisfactory explanation for the scurred and horned individuals that are produced when homozygous polled animals are mated to horned." To explain the inheritance of polledness, scurs and horns, White and Ibsen elaborate the following hypothesis: All cattle are homozygous for the gene for horns, H. The native cattle of Africa have in addition another factor for

horns, Ha. Polledness is due to a dominant gene, P, which is completely epistatic to HH in both sexes. The scurred condition is supposed to be caused by a gene, Sc, which is epistatic to P in the male, whether homo- or heterozygous, but in the female it is epistatic only in the homozygotes (ScSc). In horned animals, HH is epistatic to Sc in both sexes. White and Ibsen show how this hypothesis accounts for all aberrant cases in crosses between horned and polled breeds, *e.g.,* the appearance of horned F_1 individuals as well as scurred or horned animals from matings where one of the parents was clean polled and the other one horned.

The present writers, however, are aware of only one case where an F_1 individual with "solidly attached" horns has appeared, in controlled experiments, after crosses between polled and horned breeds of *Bos taurus* (Gowen, 1918). Also when polled breeds of *Bos taurus, e.g.,* Aberdeen-Angus, are crossed with Brahman cattle (*Bos zebu*), or bison (*Bison bison*) or yak (*Poëphagus grunniens*) the polled character is strongly dominant in F_1 (Black, 1936; Deakin, Muir and Smith, 1935). In the F_1 generation from the Angus $\times$ Brahman cross carried out at the field station located at Jeanerette, Louisiana, all the bull calves had either short horns or scurs (Black, 1936). It would not be surprising if in such rather wide crosses the results differed somewhat from those obtained in crosses between breeds within the same species or subspecies. The frequency as well as the size and shape of scurs appearing in heterozygous animals from breed crosses show a great variation, from slight bone protuberances on the skull and very small keratinous developments of hair tufts on the skin above the horn locus, to big loose or tight scurs. The degree of scur development is dependent on the sex of the animal, the scurs, on the average, being much more strongly developed in the male than in the female. Heterozygous F_1 females, and in some few cases also males, may be clean polled. The variation

between animals of the same sex is probably due to modifying genes, which perhaps only indirectly affect the development of horns and scurs, by determining the time at which the tissues of the horn bud started to differentiate in relation to other tissues. There is a striking variation in, and between breeds of cattle in the size and shape of the horns, and in the shape of the skull, and this variation is probably largely controlled by genes. Why should not the same and a number of other genes control the development of scurs? If there are numerous modifying genes influencing scur formation and horn growth, nothing can be gained by assigning one genetic symbol (*Sc*) to this multitude of genes.

There exists a century-old controversy over the nature of horn growth, centering largely around the question of whether the horn core is apophyseal in origin—*i.e.*, whether it is simply an outgrowth of the frontal bone—or whether it is epiphyseal, originating as a separate ossification which later becomes attached to the skull. Further, as regards the keratinous sheath of the horn, some have maintained that its development is initiated by the growth of the bony part below, others that the primary stimulus resides in the skin, the development of the keratinous structure stimulating the bone development, while still others are inclined to the view that these structures are largely independent in so far as their initiation is concerned. Dove (1935) has reviewed the whole subject in the light of his own experiments in which he transplanted the various tissues concerned. His general conclusions have a direct bearing on the genetic interpretation of horn inheritance.

The transplantation experiments were carried out at the department of genetics, University of Wisconsin, partly in the cross-breeding herd. Dove's experiments would appear to have established quite conclusively that the primary stimulus for the development of the bony part of the horn, or horn spike, including certain changes

in the shape of the skull contiguous to the horn, resides in the connective and dermal tissues at the horn locus, and consequently above the periosteum of the frontal bone at that point. This epiphyseal center of ossification is the *horn bud* or *horn nucleus*. In a new-born calf, that is destined to be horned, it is still above the frontal periosteum, which is intact at that stage; but it appears already to have exercised an inductive influence on the underlying frontal bone, so that a small protuberance or boss is formed, which later becomes the basal part of the horn. Within a short time the periosteum underlying the horn nucleus is dissolved away and the ossifying activity of the *os cornu,* formed by the horn bud, becomes confluent with that of the frontal bone so that it is not recognizable as a separate ossification. Transplantation experiments showed that the tissues of the horn bud placed in contact with the periosteum at other points on the skull had the ability to dissolve the periosteum and form a horn spike at the new location.

At the time of birth the skin above the horn bud has not yet keratinized, but it would appear that potentialities for formation of the horn sheath have already localized in the epidermis at the horn locus, since keratinization proceeds even if this tissue is separated from those which underlie it. The development of a normal horn depends on the subsequent harmonious interaction of the parts mentioned, *viz.,* the *os cornu,* the frontal bone at this locus, and the keratin epidermis.

In clean-polled breeds such as the Angus the inductive and growth potentialities of the horn nucleus appear to be completely inhibited, and this is assumed to be due to the action, in homozygous condition, of an inhibitory gene, *P*. In such animals consequently there is no incipient horn boss on the frontal bone and the skull retains the unmodified shape characteristic of polled breeds. The suppressing effect of the gene for polled must begin well before birth, for keratinization of the skin at the

horn locus is also prevented. The gene *P* is not, however, completely dominant in its inhibitory action, as evidenced by the fact that in heterozygous animals resulting from crosses of polled with horned breeds the development of horn structures is not entirely suppressed. The majority of the crossbreds possess scurs in some degree of development (Figs. 1 and 2). Sex is one factor in degree of expression of scurs and subsidiary modifying genes probably also have an influence.

In animals with scurs, therefore, the horn nucleus may be looked on as having a transitory and incomplete influence. The influence in some cases is so slight as to have produced only a small keratinized "scale." When a scur is formed the nucleus is active for a longer time; it proceeds as a separate ossification center and forms an *os cornu* which may resemble a small horn spike in shape and is covered by a keratin sheath appropriate to its size. It does not normally become attached to the skull, but in spite of this its inductive influence modifies to some extent the shape of the frontal bone and causes a small boss to be formed at the horn locus.

These facts raise the question whether there is any real difference between a scur and a horn beyond the fact that the former is loose, while the latter is firmly attached. This would be a difference in degree of development, depending on the potentiality of the horn bud to dissolve the periostial membrane and unite with the frontal bone. In most crossbred animals, apparently, the nucleus is able to form horn structures but stops short of the power of penetration necessary to make the skull attachment. Occasionally, perhaps, scurs may become attached so that they in fact become horns (*cf.* Gowen, 1918). Dove's experiments show that when a horn bud is transplanted to a new site, if even a thin layer of connective tissue is left between it and the periosteum at the new locus, it may proceed to form a structure like normal horn except that it does not become attached and hence is really a scur.

When it is placed in contact with the periosteum or directly on the bone surface it makes the fusion and modifies the receptor accordingly. It is possible that in the case of scurs there is connective tissue as well as periosteum intervening between the *os cornu* and the frontal bone, and the failure of attachment may be due to the inability of the ossification process to penetrate these tissues. Judging by the transplantation experiments it seems quite likely that if the *os cornu* of a developing scur could be brought into intimate contact with the skull bone, or possibly with the periosteum, fusion might result.

* * *

A practical bearing of the relationship between different horn tissues is found in the dehorning of calves by the application of strong caustic at the horn locus shortly after birth. It is well known that while such application may completely stop all horn growth, even in such animals the poll differs appreciably in shape from that of genetically polled animals. This is doubtless attributable to residual inductive influence of the horn nucleus on the frontal bone before the caustic treatment. Again, if the horn nucleus is destroyed, but the covering skin which has been under the influence of the horn nucleus before birth is not completely destroyed a small keratinous scur without a bony base or core might be expected to develop. Or if the nucleus is not entirely inactivated a small and misshapen horn may result. For successful dehorning with caustic, therefore, it is important that not only the horn nucleus but all the epidermis above it, that may have acquired the potentiality of forming keratin, should be completely destroyed.

Conclusions

Our concept of horn inheritance in cattle may be summarized as follows. In polled cattle horn growth is inhibited by a partially dominant gene, *P*. The horned con-

dition may be considered the primitive character; the frequency of mutations of *p* to *P* is probably rather low. Sex has an influence on the degree of dominance of *P*, probably through the action of the male sex hormone, as well as on the size and shape of horns in the recessive homozygote (*pp*). An unknown number of genes act as modifiers of horn growth, and also of scur development in the polled heterozygote (*Pp*). When polled breeds, *e.g.*, Aberdeen-Angus, are crossed to breeds with "strong" modifiers for horn development, *e.g.*, Brahman or Africander cattle and perhaps also some breeds of the western hemisphere, *e.g.*, Ayrshire, a "reversal of dominance" may take place at least in the male so that some of the crossbred bulls develop horns. Reversal of dominance may be brought about by the modifying genes causing a change in the time at which the horn bud starts to exert its influence on the underlying connective tissue and the frontal periosteum. In the F_1 generation from such crosses, therefore, we may find all stages of horn development represented from "clean polled" females to males with "solidly attached horns." In most crosses between western breeds, however, the heterozygotes (*Pp*) develop only scurs. Some cases of horned F_1 animals from crosses between polled and horned breeds may be explained on the assumption that the recessive gene for horns (*p*) still has a certain, although rather low frequency in the polled breeds. When the problem of horn inheritance in cattle is examined not only from the genetic but also from the development point of view, the simple monohybrid explanation of horn inheritance would seem to be all that the present data call for.

Summary

(1) Results obtained in crosses between polled and horned breeds of cattle (Aberdeen-Angus $\times$ Jersey and Holstein-Friesian) are in conformity with the commonly accepted hypothesis that there is a gene (*P*) which acts

as an inhibitor to the development of horns. This gene is strongly but not completely dominant to its allele (p). The recessive (pp) has normal horns. The size and shape of horns, as well as the development of scurs in the heterozygotes, are influenced by a number of modifying genes.

(2) Approximately 60 per cent. of the F_1 animals were scurred and most of the others had protuberances of varying size on the frontal bones. A few F_1 cows had, however, clean polled skulls. Scurs were more frequent and more strongly developed in males than in females, and this was particularly true of bulls raised to mature age. Scurs occurred also in many of the F_2 animals but others were clean polled. It is suggested that in some breed crosses, *e.g.*, Angus $\times$ Brahman or Africander cattle, scurs may become attached to the frontal bones and thus develop to true horns.

(3) The horned segregates, particularly from the Jersey $\times$ Angus cross, had horns of larger size and different shape than those of the horned parental breed, this modification apparently being due to factors brought in by the Angus breed.

(4) The long and relatively narrow, primigenius type of skull of the Holsteins is dominant in F_1 over the shorter, brachycephalous skull characteristic of the Angus breed. There is some evidence of segregation in the F_2 generation.

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ANIMALS AND SALINITY IN THE GREAT BASIN[1]

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INTRODUCTION

THE Great Basin of western North America is an arid geographic province isolated from the sea. The aridity of this isolated region has resulted in the accumulation of very high concentrations of certain salts in the low areas of the region, and this in turn has profoundly affected the nature and distribution of plants and animals in the saline areas. The purpose of this article is to present a general consideration of the ecological significance of the salinity characteristics of the region and to indicate the tremendous possibilities that exist here for fruitful ecological and physiological research.

Experiments reported from various parts of the world have shown that salinity may act as an ecological factor in the lives of animals not only directly by its presence in the water in which they live or which they drink, but also indirectly through its presence in soil or soil water by affecting the distribution and floral composition of the plant cover with which they are associated.

Further analysis of the direct effects on animals reveals that sudden variations in the composition or concentration and even the gradual attainment of certain high or low salt concentration levels may reduce the vitality or even kill animals that live in it or have to drink it, and may prevent the establishment of additional species. There appears to be an optimum salinity both as to quality (chemical composition) and quantity (total concentration) for each species involved. In all probability, the range of conditions that may be considered optimum

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varies with different species and doubtless, also, the sensitivity of each species may differ at different stages of the life cycle.

Beyond the optimal limits, further changes in the salinity composition and concentration (quality and quantity) eventually reach maxima with greater concentration because of evaporation or minima with lesser concentration resulting from dilutions from rain water. Conditions approaching these limits may be called pessimal. Beyond these limits, animals usually fail to survive.

Salinity Conditions in the Great Basin

For animals, distilled water is a very unsuitable medium in which to live. The equivalent rain or snow water which accumulates in mountain tops does not long remain in a pure state. It is a good solvent and soon picks up available solutes in the form of either gases or solids from adjacent air or soil. The dissolved solids usually include substances that have to do with salinity, which is here regarded as including all salts in solution and is thus much more inclusive than the saline salts of the basic metals of the alkali group.

Extremes approaching pure snow water are found in mountain streams and lakes such as those of the Uinta Mountains of Utah with substrata of quartzite and those of the Sierra Nevada Mountains along the Nevada-California border, which are in some cases so low in concentration and so restricted in composition that the fauna is meager. As water stands in mountain lakes, runs down mountain sides or percolates through subterranean routes, salinity tends to increase by further solution of salts from soil or rocks.

Fresh-water lakes, such as Utah Lake and many artificial lakes (reservoirs) serve as temporary storage, where time is available for further work of solution from the substratum or from suspended sediments. At the foot of the mountains in the Great Basin, streams consolidate, gradients decrease, temperatures rise and salin-

ity further increases. Valley streams, in general, may be characterized in contrast with mountain streams as warmer, more sluggish and of greater salinity.

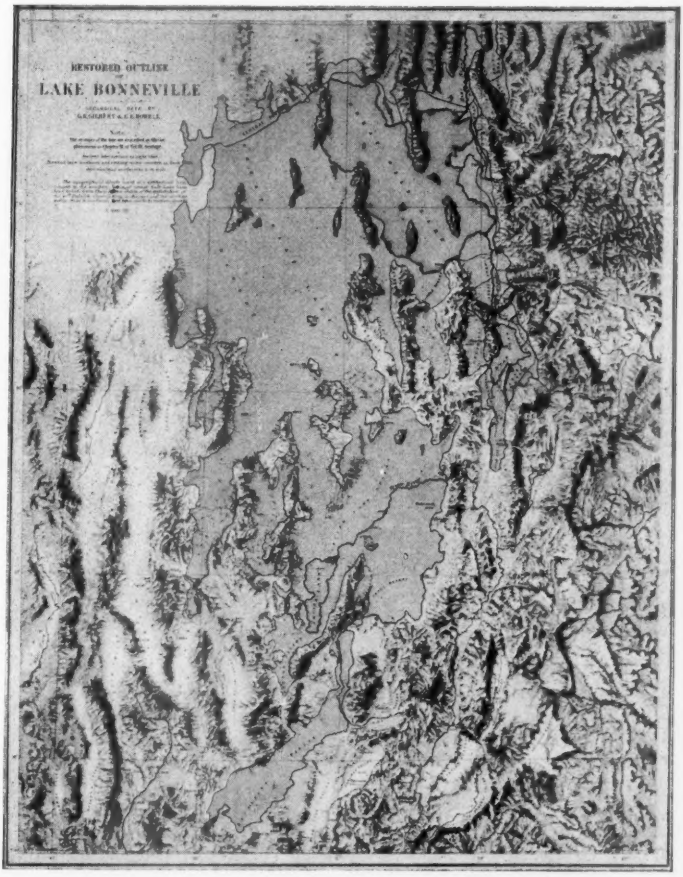

FIG. 1. Gilbert's map of old Lake Bonneville, showing its drainage basin, its outline and its remnants in Sevier and Great Salt Lakes.

Since there is no outlet to the ocean, all water, all sediments and all solutions are accumulated somewhere in the basin, usually in the valley bottoms. Here the stream gradient is so nearly horizontal that many stagnant ponds

or marshes through which water moves very slowly occur around the borders of the ultimate lakes, ponds or playas from which water escapes by evaporation. Here also, underground waters tend to reach equilibrium with these ultimate lakes and form underground water tables at short distances beneath the terrain surface, usually within reach of plant roots in the nearly level bottom lands.

The lowest basin depressions, such as Great Salt, Sevier and Little Salt lakes in the Bonneville Basin (Fig. 1) and Winnemucca, Pyramid, Honey, Humboldt, Carson and Walker lakes in the Lahonton Basin having no drainage outlets, are in effect shallow "evaporation pans." It is here, where water is removed only by evaporation and minerals have no outlet, that final concentration in salinity occurs.

In general, the salinity constituents in these various subbasins are qualitatively identical with those of the ocean, but instead of being constantly proportional as in all sea water, both the amount of concentration and the proportion of individual salts present varies from place to place. These concentrations range through many gradations up to complete saturation of certain salts (*e.g.,* sodium chloride) in certain lakes.

The differences in concentration arise from different interactions of factors in the different sub-basins. Some drainage systems cover igneous rocks with low soluble salt content. Others cover marine sediments containing heavy salt concentrations and still others contain "mineral springs" arising presumably from deep underground sources mainly along fault lines. Taking the basin as a whole, the waters run almost the entire gamut from practically pure snow water through nearly all gradations of salinity to complete saturation of certain constituents and to deposits of excess quantities of soluble salts in certain soils.

Stabilized conditions of salinity such as those of the ocean are not to be expected in the Great Basin where there have been drastic changes in the climatic history

and consequent changes in salinities of waters. Russell (1885) holds that Lake Lahontan has never had an outlet and has consequently fluctuated up and down with climatic cycles. Gilbert (1890) holds on the other hand that Lake Bonneville overflowed into Snake River in southern Idaho at first but that, since desiccation lowered the lake below its outlet, it too has fluctuated up and down with climatic cycles.

The nature of present-day fluctuations is revealed in historical records of Great Salt Lake (a remnant of Lake Bonneville) which are available since Mormon pioneer settlement was made nearly a century ago. Fluctuations in the lake level are shown in Fig. 2. Analyses of the

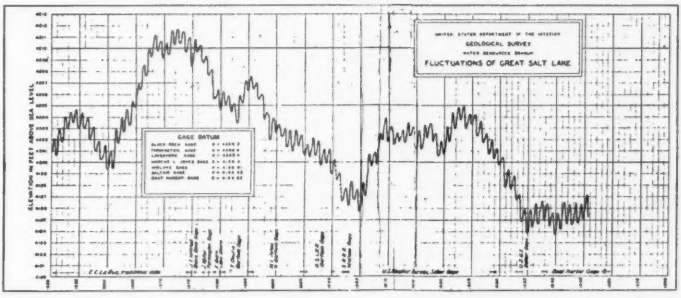

FIG. 2. A graph showing fluctuations in the level of Great Salt Lake since 1850. Data prepared by U. S. Geological Survey.

lake water made from time to time indicate an inverse correlation between lake level and salinity (Clarke, 1924). Salinity indicated in 1869 when the lake was close to its highest historical level as shown in the chart was in round numbers 15 per cent, and again in 1877 at about the same level a little less than 14 per cent. By contrast, the salinity in 1940 when the lake was near its lowest historical level was more than 27 per cent. The difference between maximum and minimum salinity is in round numbers 13 per cent and the difference in lake level between those two extremes is about 13 feet. It thus appears that within these limits there is approximately an in-

crease of 1 per cent in total salinity for each one foot decline in lake level or *vice versa.*

Similar fluctuations of lesser significance and of much smaller quantitative relations probably occur in so-called "fresh water" streams and lakes in the Great Basin as they do elsewhere. The salinity of streams and freshwater lakes would be considerably reduced during high-water periods from melting snows or rains unless the excess high water produced erosion and carried silt from which soluble salts could be extracted. Otherwise, the salinity would be higher in such waters when they were derived from underground sources such as springs and seepage.

Salinity Problems of Organisms

In general, it seems that organisms living in these waters are sorted out in accordance with the optima they seek or within the limits they can endure if optima are not available. However, when this hypothesis is tested by critical study of individual cases, it appears that many things in detail tend to prevent organisms from reaching environments that have optimal conditions of salt type and concentration as well as other necessary items such as temperature and available oxygen.

When living in sub-optimal conditions, there must be constant struggle on the part of the hereditary potential of organisms with the exigencies of the environment (in this case the exigencies of salinity) to keep the organism functioning under the handicaps. Fluctuating salinity would tend alternately to intensify or ease the struggle from time to time. Natural selection probably operates very effectively in the periods of intensified struggle, and the probabilities indicate that the evolutionary process would proceed at a relatively rapid pace under such circumstances.

It is well understood in genetics that there are hereditary variations in many characteristics. The works of Sumner (1906) and of Young (1941) have shown that

there is considerable variation among the members of given species in their abilities to withstand fluctuations of salinty. No doubt, those which reach their limit of tolerance first will perish before others with greater limits of tolerance during such fluctuations in salinity and thus leave those that can withstand the sub-optimal conditions to survive and propagate their hereditary survival characteristics. This would tend toward better adaptation in subsequent generations of the population to survive sub-optimal conditions, which in turn would thereby tend to become nearer optimum for the modified population.

This process of adaptation through natural selection is doubtless aided by gene mutations and chromosome aberrations but under any conditions, it seems to be a slow process. Under fluctuating conditions of salinity such as those of the Great Basin, it would be expected that adaptations would tend toward more wide-ranging limits of tolerance in salinity than in the ocean where salinity conditions are so stable. This would make an interesting research problem.

In the stable conditions of the ocean, many of the primitive organisms have the cells of the body exposed to the sea water and osmotic exchanges are made directly with it. With increase in complexity of the more highly organized forms, there is generally an increasing separation of the internal environment from the external by enclosing the body within a more or less waterproof coat and relegating the osmotic exchange to specialized cells that are usually associated with gills or kidneys.

In terrestrial animals, this separation of internal and external environment is more highly developed, but the internal environment is constantly being upset by intake, excretion and secretion and automatic thresholds are established that tend to hold it level. "The conditions under which cell life is possible," according to Baldwin (1940), "are very restricted and have not changed substantially since life first began. . . . The subsequent

evolution of different forms of life has necessarily been attended by that of mechanisms for maintaining within the animal an environment with the properties required for the continued life of its cells."

Salinity Problems of Aquatic Animals

Animals living in any medium must be able to regulate osmotic exchanges so as to maintain the conditions necessary for life. Obviously, the type of regulation will vary with the adaptations the animal possesses and the salinity of the medium involved. Animals adapted to marine life that go into fresh water will have a different problem from those adapted to fresh water that go to live in the ocean. Baldwin (*ibid.*) compares marine and fresh-water fishes as follows:

(1) Fresh-water teleosts have internal osmotic pressure greater than the external so that the osmotic exchange in the gills permits water to enter from the outside tending to dilute the blood. This in turn permits a hypotonic urine to pass out of the kidneys.

(2) Marine teleosts living in a medium with salinity of about 3 per cent have an external greater than the internal osmotic pressure and consequently uses a different physiological method. The fish drinks water absorbing both salts and water. The salt is eliminated by special cells of the gills. The water then passes as an isotonic urine out the kidney, which has few glomeruli.

(3) Marine elasmobranchs (sharks) have internal and external osmotic pressures about equal. The problem of excretion is solved by allowing about 2 per cent urea to accumulate in the blood, which then brings water in through the gills and allows a slow stream of nearly isotonic urine to pass out the kidneys.

(4) Fresh water elasmobranchs use much the same system but maintain only about .6 per cent of urea in the blood. With internal osmotic pressure greater than the external, water enters via the gills and passes out the glomeruli of the kidneys.

Sumner (1906) in his work on fishes called attention to the fact that some animals live in water in which salinity is in approximate osmotic equilibrium with that of the blood, while others that have blood and water pressures vastly different are able to do so by biological control of osmotic processes. Apparently such control is exercised only within narrow limits for a given species and the amount of such control varies considerably among different species.

Scott (1910) showed, in the case of *Fundulus heteroclitus,* a species of killifish living along weedy shores or in brackish waters and presumably having some degree of osmotic control, that when transferred from sea water to fresh water its blood was diluted, but when placed in salinities much greater than sea water, its blood was concentrated. Dilution was indicated by decrease in the number of blood corpuscles per unit volume, lowering of hemoglobin percentage, lowering of specific gravity and raising the freezing point of the blood.

Sumner (1906) also found that some fishes which apparently had little control over the osmotic processes not only absorbed water which diluted the blood but also lost salt, and he concluded "one factor in the death of salt water fishes in fresh water is the extraction from their tissues of an amount of salts sufficient to reduce the percentage below a certain necessary minimum." He found further that osmotic control was much more difficult to regulate in distilled water than in water which contained a small amount of sea water salts.

It would appear from this that Great Basin species living in "fresh" water of low salinity might sometimes be subjected to periodic dilutions of the water to such an extent that deleterious effects might ensue. Since the water of streams increases in salinity along its path downward such effects would be more pronounced up stream. Those animals living further down would find less difficulty and deleterious effects would be correspondingly reduced. Those living in the region of optimal conditions should be better able to maintain themselves satisfactorily than those along the fringes near the minimum. Thus low salinity would tend to set one limit to the zone in which they could live provided other things are suitable.

At the other extreme, that of excess salinity, the danger seems to be in reverse direction. Instead of extracting salts from the blood to a dangerous degree as in water of minimum salinity, excesses in the water bombard the ani-

mal with so much saline material that too much of it gets into the blood so it can not be properly manipulated in the physiological processes. In some cases, the absorbed materials may actually be toxic. Sumner (1906) indicates that "it is the chemical nature of the solutions used rather than their osmotic pressures which determines, in many cases, whether they shall prove fatal."

In this connection, Raber's (1926) analysis of certain relations between kations and anions of solutions and plasma membranes suggests that such relationships may have a great deal to do with osmotic relations of animals living in saline waters. In fact, it seems possible that the great changes or variations of salinity concentrations in some lakes may produce sufficient change in the ionic content of the water to so upset the osmotic processes of some organisms as to lead to fatal results. This offers a large field of exploration.

Studies of the brine shrimp, *Artemia salina* (or *A. gracilis*) of Great Salt Lake throw some light on this problem. Jensen (1918) tried rearing shrimps from eggs in 9 different concentrations ranging from normal salt lake water of March–May, 1916, through several dilutions to distilled water and through several concentrations by evaporation to complete saturation. Eggs were planted in the solutions on March 28 and kept at room temperatures.

In distilled water, the eggs hatched readily in less than 24 hours but the nauplii lived only from 1 to 3 days. Eggs hatched within two days in the greatest lake water dilutions with specific gravity of 1.027 (4 per cent), 1.044 (6 per cent) and 1.064 (9 per cent). It took 13 days in the next dilution 1.085 (12 per cent) and 16 days in the lake water 1.109 (15 per cent). A few eggs hatched in the concentrated brine 1.130 (17.4 per cent) on May 5, 38 days after planting. None hatched in the nearly saturated concentrations 1.171 and 1.179.

Further study and checking of results by transferring both eggs and nauplii from one solution to another led

him to conclude that the dilutions of 6 to 12 per cent "seemed to be the most favorable for the growth of *Artemia*" in all stages of development. This was apparently better than the lake water itself in which the shrimp normally lived. It has already been indicated that salinity of the lake ranges from nearly 14 to 28 per cent. On the basis of Jensen's experiments, one would expect that the numbers of shrimp hatching in a given length of time would be far greater in years when the lake level is high and the solutes are dilute, than when the lake level is low and the solutes are concentrated. So far as known this has not been tested under natural conditions.

Studies so far discussed have dealt largely with total concentrations of salinity. Other investigators have probed into more detailed questions concerning the effects of various components of salinity. Countance (1882) after studying effects produced by changing the composition of sea water came to the conclusion that "every modification in the composition of sea water" (if carried far enough) "finally becomes fatal to these animals." Could this explain the absence of mollusks from Great Salt Lake?

Quinn (1940) reviewed certain literature dealing with chemical effects on *Artemia salina* and reported her own investigations. Particular attention was given to the effect of the magnesium ion in different concentrations in relation to (1) emergence of the nauplius from the hard shell but still enshrouded in the nuchal membrane and (2) the hatching from this membrane in which the free-swimming nauplius is released. In normal sea water at 25° C, emergence takes about 12½ hours and hatching about 7 hours. Increase of the magnesium ion concentration up to 200 per cent did not affect the time of emergence but hastened the hatching from the membrane. Decrease of the concentration hindered and finally prevented hatching.

Whether the optimum salinity and the pessimal limits remain constant throughout life or whether they change from time to time during development are questions

which appear to have received scant attention. It seems obvious that there must be some changes in migratory fishes such as the salmon which spend their early and late life in fresh water and the intervening period in sea-water, or the eels and lampreys that reverse this procedure.

Chamberlain (1907) reported some experiments by Rutter in which it was demonstrated that king salmon fry did not survive a five-hour trip from fresh water into sea water but that 94 per cent of the larger fingerlings did. The probable explanation is that the young fish develop the ability to withstand the shock of such change about the time they would normally enter the ocean.

Young (1941) investigated the ability of gametes and larvae in comparison with the adults of the California mussel to withstand reduced salinities of the water in which they lived. It was found in experiments reported by Fox *et al.* that the larvae suffered more deleterious effects than adults in salinities of less than 2.96 per cent.

The waters of the Great Basin run the gamut of salinity from fresh to saturated. The streams and fresh water lakes are much more stable with much less fluctuation than the saline lakes on the floor of the basin. According to data analyzed by Clarke (1924), none of the basin waters approximates sea water in salinity concentration. Intermediate conditions between fresh and salt are of course found at the mouths of rivers that empty into Great Salt Lake, but the mixing zone is so unstable that no constancy can be found.

Moore (1900) investigated the possibilities of introducing into these mixing zones marine animals such as oysters to study possibilities of commercial development. He found that animals so introduced would be subjected to fluctuations of salinity far beyond the lethal limits because of three sets of circumstances: (1) the variable quantity of inflow of the rivers which would push the mixing zone out in high water and allow it to move back during low water, thus changing salinity semi-annually at a given point, (2) the diffusion difficulties of mixing

fresh water with the brine, the fresh tending to overlay the heavier brine and often running out in large tongues which tended to shift from place to place, and (3) the changes in lake level from year to year which shifted the shore line.

He did, however, find that certain mineral springs might by artificial dyking and concentration by evaporation be made to resemble sea water sufficiently for such animals to survive but considered the cost so excessive as to be uneconomical.

So far as known, no one has attempted a classification of animals of the Great Basin water from the standpoint of salinity tolerance, and this would make an exceedingly interesting research problem. There seems to be little doubt that each species has a different range not only of the optimum but also of the tolerance limits. It seems certain that some species are sorted out in different habitat niches within the limits set by salinity.

If animals immersed in water differ in blood salinity from that of the water, there must be organic machinery to regulate the differences. Bernard, quoted by Sumner (1906), states that

> In all living beings the internal medium, which is a true product of the organism, preserves the necessary relations of exchange and of equilibrium with the external cosmic medium, but in proportion as the organism becomes more perfect, the organic medium specializes and isolates itself, in a certain manner, more and more from the surrounding medium.

Hesse, Allee and Schmidt (1937) boldly state that animals "must be protected from osmotic changes in the salinity of their body fluids, either by an impenetrable surface or by the ability to eliminate excessive amounts of salt or water through their excretory organs." Sumner's (*op. cit.*) investigations seemed to indicate that it was the gills of fishes and not skin nor digestive system that was involved in the regulative mechanism. It seemed probable that there were different degrees of permeability in gills which might help to account for different abilities in different species.

The Salinity Problem of Land Animals

Animals living on the land have a different problem. They are not surrounded by water and neither skin nor lungs are exposed to the osmotic pressures involved with salinity. Their chief contact with salinity is in drinking water, and for herbivores, in the cell sap of plant parts that are browsed; both of these are handled by the digestive tract and kidneys. Since water intake is voluntarily controlled, it would not be expected that an animal would get so much water as to cause difficulties from excessive dilution of the blood. The problem, if any, is generally in the other direction.

Excess salinity presents definite problems that must be regulated in order to replenish water lost from the blood by evaporation or excretion. It is well known that waters of high salinity such as those of the salt lakes are useless as sources of drinking water for the great majority of animals. Fresh water sources are usually satisfactory. Mineral springs are in a debatable position.

Meinzer (1911) says in relation to human water consumption: "Small amounts of the common mineral constituents are not harmful to health. Chlorides are not objectionable in drinking water if only 50 to 100 parts per million are present, but amounts clearly perceptible to the taste render water unpalatable. Magnesic and sodic sulphated waters are laxative and very high magnesium or sodium content renders water unfit for man or beast. The worst form of water is that which contains alkali carbonates." No doubt, lack of suitable drinking water would bar many animals, especially certain vertebrates, from large parts of the Great Basin.

Salinity plays a prominent role in the distribution of certain plants. Indirectly then, salinity may be considered as a factor in the distribution of certain animals when such plants act as ecological magnets or when they are more or less closely associated. Other animals, of course, are not so limited.

Figure 3 shows an ideal section from Great Salt Lake across the flats to the foothills, in which water table, soil and root relations are shown. The barren salt flats, where little if any conspicuous vegetation exists, have no animals that are known to be obligate.

The flats bearing shadscale, greasewood and other halophytes are much more attractive to animals in general than are the barren flats.[1] Many animals inhabit them as part of a broader habitat, and only a few find them to be a chief attraction. The most outstanding example of the latter type is the horned lark, a bird adapted to such open flats where vegetation is short and sparse and where it,

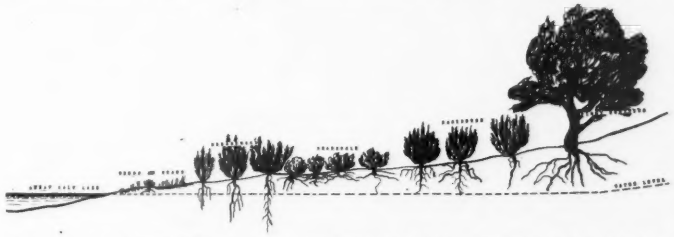

FIG. 3. A theoretical section from Great Salt Lake across the flats into the foothills. Soils of the sagebrush and pigmy conifers is well drained and without excessive salts. Drawing by Seville Flowers and the author.

like the dominant plants, tends to receive but little amelioration from the full impact of the desert environment, such as direct sunshine, winter cold and sweeping winds.

In upland localities above the salt flats, the sagebrush, pigmy conifers, shrub vegetation and coniferous forests of the mountains are all associated with low salinity of soil water, but the distribution of these communities is determined by factors other than salinity of soil water and hence the distribution of animals among them is not a function of salinity and has no place in this discussion.

RESEARCH PROBLEMS SUGGESTED

A study of the salinity characteristics of the streams, lakes and marshes of the Great Basin.

[1] See Fautin 1946.

A comparison of tolerance limits of salinity in marine organisms and related forms affected by saline conditions in the Great Basin.

The relative effect of variations in salinity on the process of reproduction in various species of animals.

A study of the tolerance limits of salinity in the development of larvae and pupae of the brine flies, *Ephydra hians* and *E. gracilis.*

A study of salinity tolerance limits of mollusks, worms and insect larvae of the streams, lakes and marshes.

A study of salinity tolerance limits of various kinds of fishes.

A study of salinity tolerance in the amphibians.

A study of the effect of variation in the salinity components upon various aquatic organisms.

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RED EYE PIGMENT DETERMINATION IN THE LOZENGE ALLELIC SERIES OF *DROSOPHILA MELANOGASTER*

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THE concept of a comparative study of the members of a series of multiple alleles as a means of shedding light on the problem of gene action is not a new one; phenotypic studies along these lines have been carried out by a number of workers. In fact, the series used in the work reported here has been extensively studied in this fashion. However, in the present work a new mode of attack is employed, in that quantitative measurements are added to the subjective phenotypical descriptions. As will be seen, these quantitative analyses sometimes corroborate exactly the subjective descriptions, but in other instances they do not; in these latter instances we are therefore led to search for the additional factors which are concerned in the determination of the phenotype.

The multiple allelic series forming the basis for these studies is that at the lozenge locus on the X chromosome of *Drosophila melanogaster*. Mutations at the lozenge locus are characterized phenotypically by modification of the eye size, structure and color (Oliver, 1947), by abnormalities of the female genitalia and an accompanying decrease in fertility (Oliver and Green, 1944; Anderson, 1945), and by alterations in the pulvilli and claws of the tarsi (Oliver, 1947).

Seven of the ten available members of the lozenge series have been analysed with reference to the quantity of red pigment present in the eyes, as well as to the quality of that pigment in comparison with the normal. These seven alleles are: lozenge (lz), lozenge-37 (lz^{37}), glossy (lz^{g}), lozenge-Bar Stone (lz^{BS}), lozenge-34 (lz^{34}), lozenge-y^4 (lz^{y4}, and lozenge-3 (lz^{3}). The method of analysis followed was essentially that of Ephrussi and Herold (1944)

for the determination of the red eye pigment of Drosophila, with the exception of minor discrepancies. The gene for vermilion eye (*v*) was introduced into the genomes of all the lozenge alleles in order to prevent the deposition of brown pigment in the eyes, and thus avoid the possibility of error due to the fact that the brown pigment is partially soluble in the solvent used to extract the red component. Flies of the genotype *v f* (vermilion, forked) served as controls. All extractions of pigment were made in 10 ml. of solvent (30 per cent ethyl alcohol acidified to pH 2 with concentrated HCl), filtered through

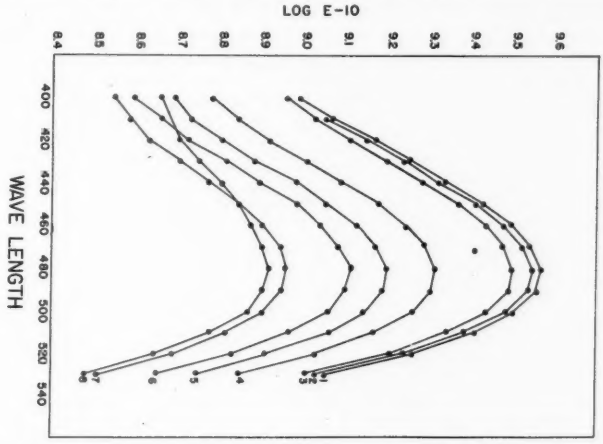

FIG. 1. Absorption curves of red eye pigment. Ordinate: log of extinction; abcissa: wavelength in millimicrons. The numbered curves represent the following mutants: 1, *v;* 2, lz^{37}; 3, lz^{9}; 4, lz^{88}; 5, *lz;* 6, lz^{34}; 7, lz^{v4}; 8, lz^{3}.

Schleicher and Schull paper number 597, and measured in a Coleman Universal spectrophotometer, model 11, against a solvent blank. Every possible precaution was taken to insure uniformity of developmental conditions. The flies were raised at a temperature of $23 \pm 1°$ C; crowding of the cultures and resultant nutritional deficiencies were carefully guarded against. Furthermore, since it has been demonstrated that the quantity of red pigment present in the eyes increases until the fifth day

after eclosion (Ephrussi and Herold, 1944), the flies were aged for five days before analysis. Females were used in every instance.

Figure 1 represents a plot of the spectral absorption curves of the red pigment extracted from each of the seven lozenge alleles, plus the curve for the *v f* controls. The red pigment of vermilion flies has been shown to be quantitatively and qualitatively identical to that of the wild type (Ephrussi and Herold 1944). In regard to the lozenge alleles, with the exception of lz^3 the absorption curves agree closely with that for vermilion, indicating that the red pigment is similar or identical in all cases. The absorption curve for lz^3 has the characteristic maximum at 480 mu, but a discrepancy exists over the range of 400–460 mu. There is reason to believe that this discrepancy is not a real one, but rather represents the absorption of impurities dissolved in the solvent during the extraction of the red pigment. The dearth of red pigment in lz^3 individuals is such as to necessitate extraction of relatively large numbers of heads (140 or more) in order to get sufficient pigment for measurement. Such extracts showed a marked Tyndall effect, indicating impurities. Moreover, it was noted that when large numbers of heads (in excess of 100) of other alleles, *e.g.*, lz^{v4}, were extracted, the extracts also showed a Tyndall effect and identical discrepancies in the absorption curve occurred. Attempts to remove such impurities by filtration through double filter paper were unsuccessful.

A number of separate extractions of heads of each genotype were made in order to estimate the quantity of pigment laid down in each. The light absorbed by each extract at the wave length of 480 mu was measured in the spectrophotometer. The relative concentration may be estimated from the equation $E = \log \frac{I}{I_o} / c\ d$; where E is the extinction coefficient, I the intensity of incident light, I_0 the intensity of transmitted light, c the concentration of pigment in the solution and d the thickness of the solu-

tion. Since matched cuvettes were used in all determinations, d is constant, and it may readily be seen that c, the concentration, is then proportional to E. Calculations of E values were adjusted for 100 heads in 10 ml. of solvent. The results are listed in Table 1; these represent the averages of the several determinations. The data demonstrate that the lozenge alleles may be seriated in so far as their ability to form red pigment is concerned. Thus lz^{37} (phenotypically closest to wild type) is not appreciably different from v (and therefore from wild type) in the amount of pigment laid down. The other alleles show a marked decrease in quantity of red pigment, with lz^3 forming as little as 6 per cent, if v is assigned a maximum

TABLE 1

PHOTOMETRIC DETERMINATION OF RED EYE PIGMENT OF LOZENGE ALLELES
Wave length 480 mu. E_{100}, extinction calculated per 100 heads in 10 ml. solvent.

Genotype-homozygous ♀♀	Number determinations	Average E_{100}	Per cent of v
$v\ f$	6	0.919	....
$lz^{37}\ v\ f$	6	0.919	100.0
$v\ lz^{g}\ f^{*}$	9	0.462	50.3
$lz^{BS}\ v\ f$	8	0.382	41.6
$lz\ v$	7	0.268	29.2
$lz^{34}\ v\ f\ bb$	6	0.251	27.3
$y\ v\ lz^{y4*}$	7	0.147	16.0
$lz^{3}\ v\ f$	5	0.056	6.1

* lz^{g} lies within $In(1)dl49$; lz^{y4} within $In(1)y^{4}$.

value of 100 per cent. In the case of two of the alleles, lz^{s} and lz^{36}, extraction of red pigment could be made, but the quantity obtained was so minute as to preclude measurement even when as many as 400 heads were extracted.

DISCUSSION

Ephrussi (1945) in a study of the red eye pigment of members of the white allelic series in *Drosophila melanogaster* presented data which suggest that the red pigment differs qualitatively in the eyes of each white allele. Moreover, Ephrussi was led to conclude that the red pig-

ment in Drosophila contains at least two separate components. The data presented here indicate that the red pigment formed by each of the lozenge alleles is qualitatively the same. Wald and Allen (1946) succeeded by chromotographic methods in separating the red pigment of wild type eyes into three well-defined pigments. Two of the three have absorption maxima around 480 mu; the third has its maximum in the ultra-violet. The method used in this study of the lozenge alleles would not differentiate the two pigments with maxima at 480 mu, nor does it throw any light at all on the presence or absence of the third component which has its maximum in the ultra-violet. Thus all three of the red pigments found by Wald and Allen may well be present in the lozenge alleles. Although the present analysis has failed to demonstrate any qualitative differences in the red pigment formed by members of the lozenge series, the data in Table 1 show that one function of the lozenge genes is to determine the quantity of pigment laid down. It is apparent that the alleles vary markedly in this aspect, despite their qualitative similarity.

At the same time, it is interesting to note that the quantity of pigment formed is not the only factor affecting the phenotype. Thus, while *lz* and lz^{34} form nearly the same amount of pigment (Table 1), they may be separated phenotypically without difficulty because of differences in the distribution of the pigment in the eye (Oliver, 1947).

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